

Deep-diving and diel changes in vertical habitat use by Caribbean reef sharks *Carcharhinus perezii*

Demian D. Chapman^{1,2,*}, Ellen K. Pikitch³, Elizabeth A. Babcock², Mahmood S. Shivji¹

¹Guy Harvey Research Institute/Nova Southeastern University Oceanographic Center, 8000 N. Ocean Drive, Dania Beach, Florida 33004, USA

²Pew Institute for Ocean Science, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33133, USA

³Pew Institute for Ocean Science, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 126 E. 56th Street, New York, New York 10022, USA

ABSTRACT: Longline sampling (83 sets) supplemented with 6 pop-off archival transmitting (PAT) tag deployments were used to characterize vertical habitat use by Caribbean reef sharks *Carcharhinus perezii* at Glover's Reef atoll, Belize. Longline catch-per-unit-effort (CPUE) in 2 shallow reef habitats (lagoon <18 m depth, fore-reef <40 m depth) underwent significant nocturnal increases for sharks larger than 110 cm total length (TL), but not for smaller sharks. Nocturnal CPUE of small sharks appeared to increase in the lagoon and decrease on the fore-reef, suggestive of movements to avoid larger conspecifics. PAT tag deployments (7 to 20 d) indicate that large *C. perezii* generally increased the amount of time they spent in the upper 40 m of the water column during the night, and inhabited much greater depths and tolerated lower temperatures than previously described. The wide vertical (0 to 356 m) and temperature range (31 to 12.4°C) documented for this top-predator reveals ecological coupling of deep and shallow reef habitats and has implications for Marine Protected Area (MPA) design.

KEY WORDS: Satellite tracking · Depth range · Coral reef ecology · Marine Protected Area · Carcharhinidae

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The Caribbean reef shark *Carcharhinus perezii* is the most abundant large carcharhinid shark observed on shallow coral reefs in the tropical western Atlantic (Compagno 1984, 2002, Opitz 1996), where it has previously been recorded at depths up to 30 m (Compagno 1984, 2002). Although ecosystem modelling suggests that overexploitation of large sharks like *C. perezii* could impact community structure on shallow Caribbean coral reefs (Bascompte et al. 2005), little is known about the habitat use and ecology of this species. Shallow tropical reefs (<40 m depth) are important habitat for this species during their early life-history (Pikitch et al. 2005, Garla et al. 2006a,b), and ontogenetic changes in habitat use have been documented at Glover's Reef atoll, Belize (Pikitch et al. 2005). Small juveniles (<110 cm total length [TL]) are

more common inside the lagoon (<18 m depth) than larger sharks, which are mostly caught in relatively shallow fore-reef habitats (<40 m) adjacent to much deeper water (>400 m, Pikitch et al. 2005). Automated acoustic tracking coupled with limited stomach contents analysis revealed that large *C. perezii* routinely visit and likely forage in these shallow reef habitats (Chapman et al. 2005, Garla et al. 2006a¹). However, the proportion of time spent in shallow-reef habitats and the depth range of large *C. perezii* remains unknown. This information is important from the perspective of elucidating the ecological role of the species on coral reefs and developing place-based conservation measures (e.g. Marine Protected Areas

¹ See also *Carcharhinus perezii* under www.iucnredlist.org/search/details.php/60217/summ

[MPAs]) for this top predator, which is vulnerable to overexploitation (Compagno 1984, 2002, Garla et al. 2006a; see also footnote 1).

The objectives of the present study were to characterize the depth range of *Carcharhinus perezii* and delineate diel and ontogenetic changes in the use of 2 shallow-reef habitats at Glover's Reef atoll (i.e. lagoon <18 m, fore-reef <40 m). This was achieved using a combination of fishery-independent longline sampling at this site and pop-off archival transmitting (PAT) tagging of large juvenile and adult sharks.

MATERIALS AND METHODS

Detailed descriptions of Glover's Reef atoll and the ongoing shark survey were reported by Pikitch et al. (2005). Longline gear was deployed during sampling expeditions conducted in May-June each year from 2001 to 2006. Surface-set lines consisted of 40 to 70 baited hooks (16/0 Mustad circle) spaced at 20 m intervals, hanging approximately 3.5 m below the mainline. Set locations were categorized into 1 of 2 shallow macrohabitat types. 'Fore-reef' lines were set over the narrow fore-reef (<500 m wide) that fringes Glover's Reef, in 6 to 40 m of water. The fore-reef abruptly drops off in a wall formation at Glover's Reef, quickly exceeding 400 m. 'Lagoon' lines were set inside the atoll, in 3 to 18 m of water over mixed seagrass, soft-bottom and patch-reef substrates. Each longline set was categorized as 'day' or 'night' based on the recorded set and haul times. Log-transformed catch-per-unit effort (CPUE [no. sharks 100 hooks⁻¹ h⁻¹]) was determined separately for 2 size categories; juvenile sharks <110 cm total length (TL, measured on a straight line from the rostrum to the tip of the upper caudal lobe) were defined as 'small', while larger juvenile and adult *Carcharhinus perezii* >110 cm TL were defined as 'large'. These categories follow those used by Pikitch et al. (2005) and Garla et al. (2006b) for elucidating ontogenetic habitat use patterns in this species. Sharks were also assigned maturity based on clasper size and calcification in males (Pikitch et al. 2005) and the size at maturity (200 cm) given by Compagno (1984) for females. To test whether time of day, habitat, or the interaction between these 2 factors had significant effects on log-transformed CPUE of small and/or large *C. perezii*, ANOVA tests were performed using SPSS version 13.0 for Windows. Year effects were not examined because Pikitch et al. (2005) previously demonstrated that this factor had no effect on log-transformed CPUE from 2001 to 2005.

Five adult *Carcharhinus perezii* (3 males of 170, 192, 193 cm TL, and 2 females of 210, 230 cm TL) were fit-

ted with PAT3 tags (Wildlife Computers) during May 2003 at Glover's Reef. In June 2005, a large juvenile female (183 cm TL) was fitted with a PAT4 tag on the coast of nearby Turneffe atoll (Fig. 1). Tags were attached using a 100 kg-test, abrasion-resistant monofilament bridle threaded through the base of the first dorsal fin, approximately 10 cm from its trailing edge, and secured with 2 stainless steel crimps. PAT tags archived ambient depth and temperature every 1 min of deployment and transmitted 3 h summaries in pre-programmed bins. They also provided minimum and maximum depths and temperature recordings for each summary period. Tags were programmed to detach and transmit data summaries 90 to 180 d after deployment. All summarized data received were manually checked for appropriate co-variation between depth, light and temperature in order to ensure that the tag was on the shark and functioning properly for the duration of the track. Detachment was recognized by constant surface depth readings. For each tagged shark, a chi-square test was used to determine whether there were significant differences in the proportion of time spent above a depth of 40 m (the approximate depth of the beginning of the reef slope) between day (06:00 to 17:59 h) and night (18:00 to 05:59 h) hours.

RESULTS

A total of 83 standard longline sets (50 day, 33 night; 36 fore-reef, 47 lagoon) were completed, resulting in the capture of 68 *Carcharhinus perezii* in the 'small' category (39 males, 29 females). Neither habitat nor time of day significantly influenced log-transformed CPUE of small *C. perezii* (ANOVA, $p = 0.55$ and $p = 0.79$ respectively, Fig. 2a); however, the interaction of time and habitat approached significance ($p = 0.065$). CPUE of small sharks was higher in the lagoon during the night, but higher on the fore-reef during the day (Fig. 2a). The same 83 standard longline sets resulted in the capture of 59 *C. perezii* within the 'large' size category (26 males, 42% mature; 33 females, 21% mature). Unlike that of the small sharks, log-transformed CPUE was significantly greater at night than in the day, regardless of habitat, and was significantly higher on the ocean reef than in the deep lagoon (ANOVA, $p < 0.0001$ and $p < 0.01$ respectively, Fig. 2b). The interaction between time of day and habitat was non-significant ($p = 0.064$).

PAT tags remained attached for 7 to 20 d before prematurely detaching and surfacing in the same general area in which the individual was released (Fig. 1). Four of the 6 tags transmitted summarized data records for the entire track (3 adult males, 1

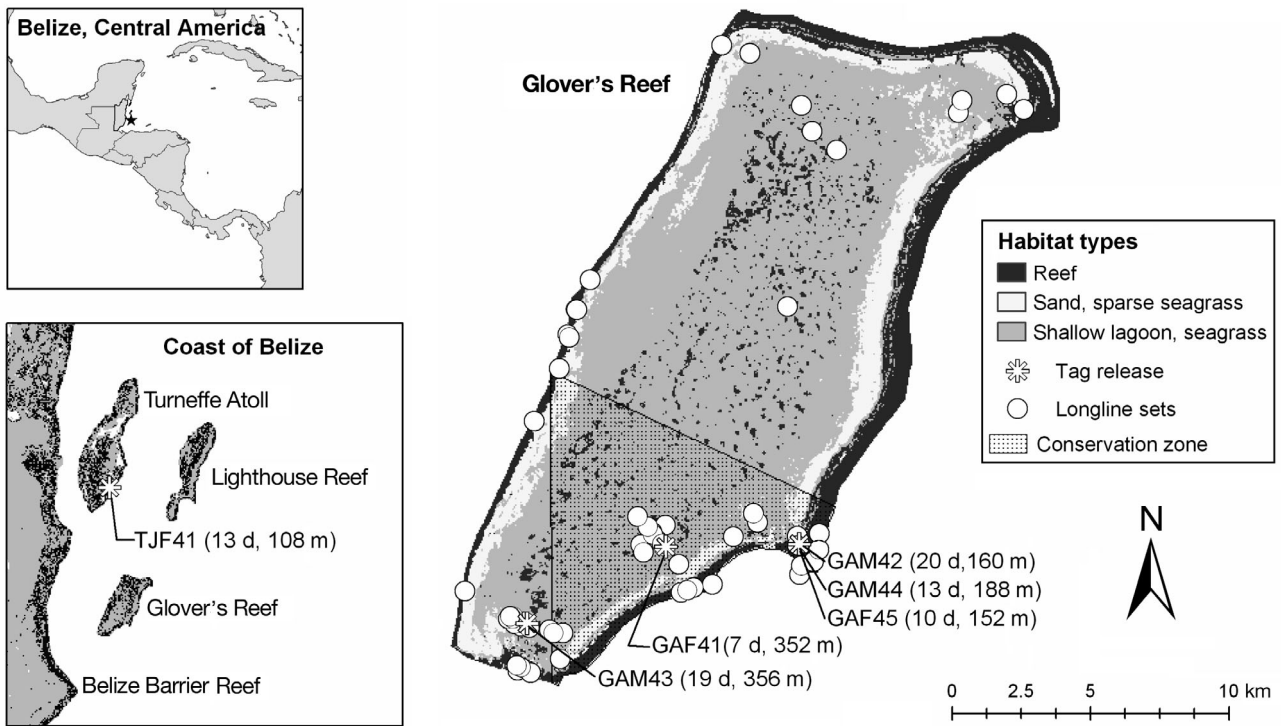


Fig. 1. Glover's Reef atoll, Belize (ca. 16° 44–56' N, 87° 42–53' W): locations of standard longlines (white circles) and release locations for PAT-fitted *Carcharhinus perezi* (asterisks) at Glover's Reef; shark ID codes are followed by track duration (d) and max. recorded depth (m). 'Coast of Belize' inset: release location and data for shark tagged at Turneffe atoll. Prefixes of shark ID codes are: G, Glover's Reef; T, Turneffe; AM, adult male; AF, presumed adult female; JF, juvenile female

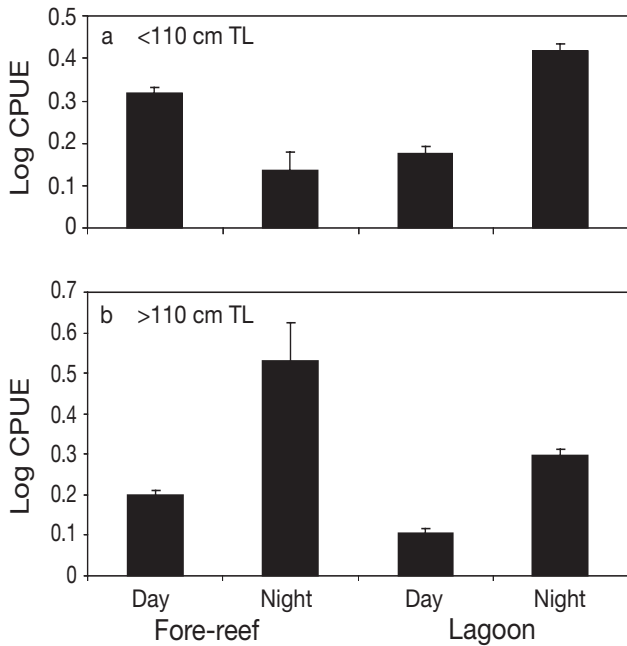


Fig. 2. *Carcharhinus perezi*. Mean (±SE) log-transformed catch-per-unit-effort (log CPUE) for (a) small (<110 cm TL) and (b) large (>110 cm TL) sharks over fore-reef and lagoon habitats during day and night hours

adult female; Fig. 3), while 2 tags only transmitted fragmented datasets (maximum depths for all sharks are shown in Fig. 1; in each case, the minimum recorded depth was at the surface). Sharks ranged from the surface down to 356 m and experienced ambient temperatures from 30.8 to 12.4°C (Figs. 1, 3 & 4). Modal temperatures experienced occurred in the 27.5 to 30°C bin for sharks GAM42, GAM44 and GAF45 (56, 68 and 84% of recordings respectively), and in the 25 to 27.4°C bin for GAM43 (63% of recordings). Modal depth ranges were 50 to 100 m for the 3 adult males and 1 to 10 m for the adult female (Fig. 3). All sharks significantly increased the proportion of time spent in the upper 40 m of the water column during night hours (χ^2 p-values were all less than 1×10^{-6} ; Fig. 3). Deep dives below the photic zone (ca. >150 m) were recorded on several occasions for all of the adult sharks, while the large juvenile female was recorded to a maximum depth of 108 m (Figs. 1, 3 & 4). A representative 5 d portion of the 19 d vertical profile of adult male GAM43 (Fig. 4) shows that this individual frequently dove to between 80 and 100 m during the track, and reached a maximum depth of 356 m. Fragmented data received from adult female G41 included a dive to 352 m.

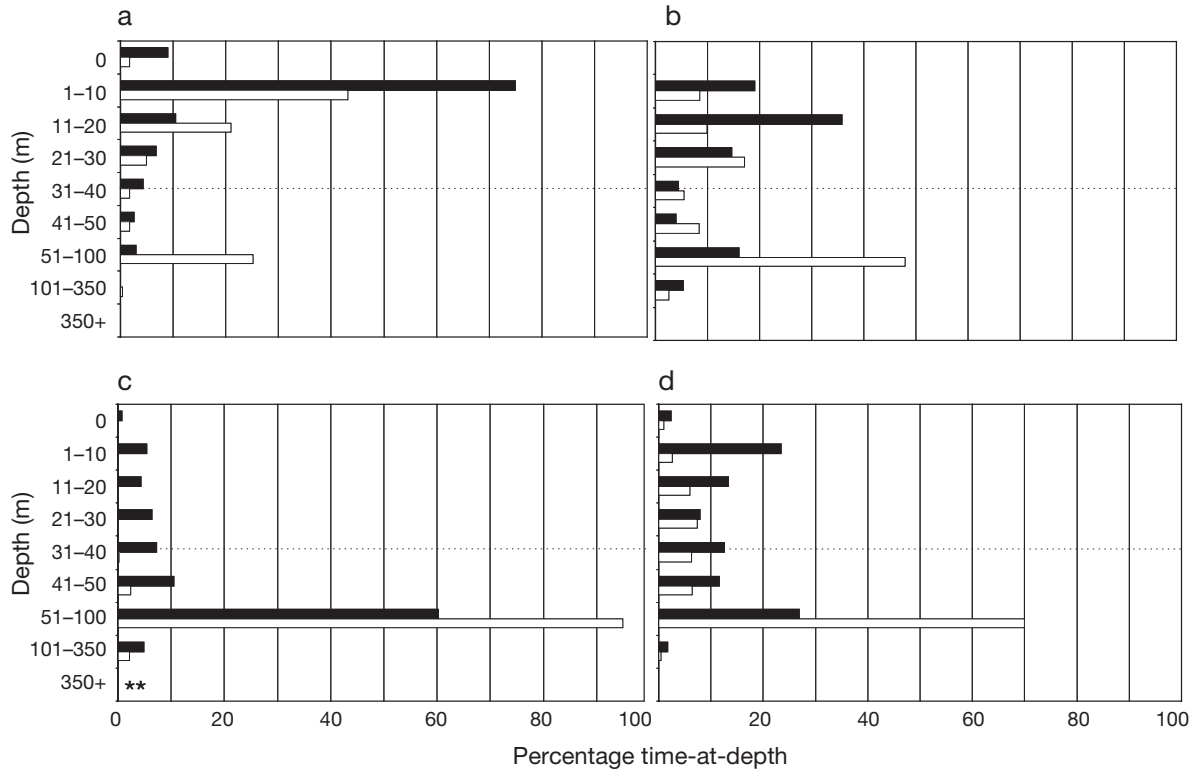


Fig. 3. *Carcharhinus perezii*. Proportion of time each shark spent within specified depth ranges over the duration of tracks: (a) adult female GAF45, and adult males (b) GAM42, (c) GAM43 and (d) GAM44. Open bars are day (06:00 to 17:59 h), solid bars are night (18:00 to 05:59 h). Dotted line is approximate average depth of the reef slope at Glover's Reef; **: bar present, but visually undetectable

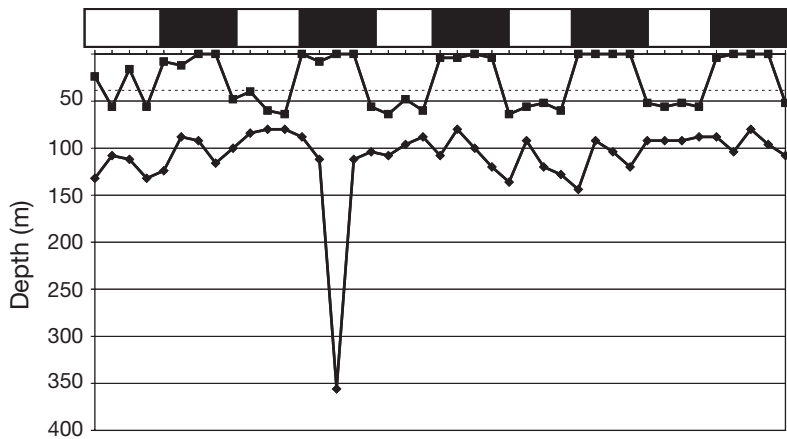


Fig. 4. *Carcharhinus perezii*. Min. and max. depths (squares and diamonds respectively) recorded each 3 h period over 5 d for shark GAM43. Bar over the x-axis represents diel phase (black, night; white, day)

DISCUSSION

Large *Carcharhinus perezii* (TL > 110 cm) were more frequently captured during the night than during the day on surface-set longlines in lagoon and fore-reef habitats at Glover's Reef, especially on the fore-reef where large *C. perezii* are more abundant. In contrast, neither time of

day nor habitat had a significant effect on the CPUE of small juveniles; however, the interaction between habitat and time of day approached significance. This suggests that small *C. perezii* occupy shallow reef habitats throughout the diel cycle, with some movement of individuals into the lagoon from the fore-reef during the night. This may reflect an anti-predatory response to an increasing nocturnal presence of large *C. perezii* over the fore-reef.

Increased nocturnal longline catch rates for sharks can result not only from diel changes in habitat use patterns but also from changes in foraging activity or catchability of the sampling gear. However, the PAT tag data corroborates an increased presence of large *Carcharhinus perezii* in waters less than 40 m at night. The PAT

tag data do not indicate a complete diel vertical migration in large *C. perezii*; rather, they suggest a tendency for sharks to increase the amount of time they spend in the upper 40 m at night. This pattern of increasing use of shallow water along with increasing depth range at night is facilitated by the topography of Glover's Reef atoll, where the shallow fore-reef is relatively nar-

row (<500 m) and drops off almost vertically to depths exceeding 400 m, allowing sharks to cover a wide vertical range with minimal horizontal movement. As a hypothesis for future studies, we speculate that an increasing nocturnal presence of large *C. perezi* in shallow-reef habitats likely brings a concomitant increase in predation risk for potential prey species, and may influence their diel habitat use and activity patterns (e.g. nocturnal refuging by parrotfish, Lindholm et al. 2006), particularly for large-bodied species that have few natural predators other than large sharks.

An accumulation of results from PAT tag deployments worldwide shows that some shark species have much wider depth ranges than previously anticipated, revealing important ecological and potential management connections between shallow and deep habitats (Boustany et al. 2002, Graham et al. 2005, Weng et al. 2005). Although our PAT tag deployments were relatively short (perhaps owing to tags catching on reef structure), they revealed that adult *Carcharhinus perezi* have a depth range that is an order of magnitude greater than previously recorded (0 to 356 m cf. 0 to 30 m). Deep-water snapper (Lutjanidae) and grouper (Serranidae) occur below the reef slope at Glover's Reef (D. Wesby pers. comm.), indicating that *C. perezi* may dive to depths of 150 to 350 m in order to feed.

Recent studies suggested that well-designed and properly enforced MPAs may provide useful conservation measures for reef-associated sharks (Chapman et al. 2005, Robbins et al. 2006). Glover's Reef Marine Reserve (GRMR) encompasses this atoll on the interior of the reef-slope, and may therefore effectively protect *Carcharhinus perezi* from fishing effort typically used to target this species in Belize (gillnets, longlines deployed in relatively shallow water of <40 m depth, Chapman et al. 2005). Because enforcement of MPA regulations is critical to the success of this strategy for shark conservation (Robbins et al. 2006), the increased abundance of large sharks over shallow water at night indicates that shallow portions of coral-reef MPAs must be patrolled by enforcement agencies at night as well as during the day. However, because large *C. perezi* often utilize depths below the reef slope and are thus outside or skirt the protected area at this site, they could in the future also be targeted with deep-water or pelagic gear immediately adjacent to GRMR. An extension of GRMR several kilometres seaward of the reef slope would therefore provide a protected zone of potentially important habitat for adult *C. perezi* and other large predators that utilize deep habitats adjacent to shallower coral reefs. We suggest that the inclusion of adjacent deep and shallow habitats within MPAs and ocean zoning plans throughout the Caribbean will provide more comprehensive protection for imperilled coral-reef ecosystems and at least one of their top predators.

Acknowledgements. This study was funded by the Wildlife Conservation Society (WCS), the Pew Institute for Ocean Science, the Roe Foundation, the Pew Fellowship Program grant to E.K.P., and a US National Science Foundation Graduate Fellowship and PADI Project AWARE grants PADI, Project AWARE grants to D.D.C. This work could not have been accomplished without the many shark-fishing teams at Glover's Reef from 2000 to 2006, with special thanks to D. Abercrombie and N. Lamb for their tireless efforts over the years. We also thank staff and managers of the WCS Glover's Reef Marine Research Station and J. Gibson for their assistance. We also thank R. Graham for walking us through PAT tag files for the first time.

LITERATURE CITED

- Bascompte J, Melian CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. *Proc Natl Acad Sci USA* 102:5443–5447
- Boustany AM, Davis SF, Pyle P, Anderson SD, Le Boeuf BJ, Block BA (2002) Satellite tagging: expanded niche for white sharks. *Nature* 412:35–36
- Chapman DD, Pikitch EK, Babcock EA, Shivji MS (2005) Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. *Mar Technol Soc J* 39:42–53
- Compagno LJV (1984) FAO Species catalogue, Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2, Carcharhiniformes. *FAO Fish Synop* 125:1–655
- Compagno LJV (2002) Carcharhinidae. In: Carpenter KE (ed) *The living marine resources of the Western Central Atlantic*. Vol 1: Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes, and chimaeras. *Am Soc Ichthyol Herpetol Spec Publ* 5:1–486
- Garla RC, Chapman DD, Wetherbee BM, Shivji MS (2006a) Movement patterns of young Caribbean reef sharks, *Carcharhinus perezi*, at Fernando de Noronha Archipelago, Brazil: the potential of marine protected areas for conservation of a nursery ground. *Mar Biol* 149:189–199
- Garla RC, Chapman DD, Shivji MS, Wetherbee BM, Amorim AF (2006b) Habitat of juvenile Caribbean reef sharks, *Carcharhinus perezi*, at two oceanic insular marine protected areas in the southwestern Atlantic Ocean: Fernando de Noronha Archipelago and Atol das Rocas, Brazil. *Fish Res* 81:236–247
- Graham RT, Roberts CM, Smart JCR (2005) Diving behaviour of whale sharks in relation to a predictable food pulse. *J R Soc Interface* 3:109–116
- Lindholm J, Knight A, Kaufman L, Miller S (2006) Site-fidelity and movement of the parrotfish *Scarus coeruleus* and *Scarus taeniopterus* at Conch Reef (Northern Florida Keys). *Caribb J Sci* 42:138–144
- Opitz S (1996) Trophic interactions in Caribbean coral reefs. ICLARM Tech Rep No. 43, Manila
- Pikitch EK, Chapman DD, Babcock EA, Shivji MS (2005) Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Mar Ecol Prog Ser* 302:187–197
- Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral reef-shark populations. *Curr Biol* 16: 2314–2319
- Weng KC, Castilho PC, Morrissette JM, Landeira-Fernandez AM, Holts DB, Schallert RJ, Goldman KJ, Block BA (2005) Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* 310:104–106